THE BIOLOGY AND POPULATION STRUCTURE OF STARLINGS AT AN URBAN ROOST[1]

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In winter Starlings (*Sturnus vulgaris*) often congregate in large numbers at special roosting places in cities where they may become a nuisance because of their noise and excrement. In the Detroit area during at least part of the winter the largest number of birds roost on the supporting beams below the Ambassador Bridge over the Detroit River connecting Detroit and Windsor, Canada. These birds follow well-established routes from the residential areas where they have fed during the day to the bridge, most of them flying in groups of 20 to 100 over the city toward the bridge. Some also come from the southeast from Canada, but usually fewer than from the Detroit side of the river. The Wayne State University campus is located along the main flight route over Detroit; and there is a lesser roost in Mackenzie Hall on the campus.

From December 1959, through November 1961, birds at Mackenzie Hall were banded, and the population structure of the roosting birds was studied. The project was terminated in November 1961, because remodeling of the building prevented further access to the roost.

We wish to thank Mr. Gordon Peace, Manager of Mackenzie Hall, for allowing us access to the roost, and to his maintenance crew for their cooperation. We also thank the following persons for their help during the project: Retta Thompson, Elsie Townsend, Roger Eriksson, Douglas Larkins, Dominic DeGiusti, Margaret Weiss, Ralph O'Reilly, Mr. and Mrs. Neil Kelley, Mr. and Mrs. Lawrence R. Lenz, and Robert Raikow. We are grateful to Stanley Gangwere for his critical reading of the manuscript.

BEHAVIOR OF BIRDS AT ROOST

Shortly before sundown groups of Starlings fly near the Wayne State University campus en route to the large Ambassador Bridge roost. Often a few birds leave the flock to join other Starlings perched and calling on or near Mackenzie Hall or flying about the roof of the building. Sometimes a few will begin to leave the flock, then change their direction of flight, and rejoin the main body going to the bridge. As the Starlings arrive in the area of the roost, either at Mackenzie Hall or at the bridge, they usually alight on prominent perches near the main roost, but not on the roost itself. Jumber (1956) has described a similar preroosting assembly of Pennsylvania Starlings. At the Ambassador Bridge many birds alight on the suspension cables of the bridge, others on a large storage tank about 200 feet away, and still

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others on power lines beside and below the bridge. At the Mackenzie Hall roost, birds alight in trees across the street from the building. The birds remain there for several minutes, calling and singing until after sundown, when they begin to fly up to the roost. There is usually a period of circling around it before alighting on it, often to rise and circle again. This process may be repeated many times before the entire group of birds is settled at dark.

Just after daybreak, well before sunrise, the birds fly from the roost, returning apparently by about the same route as they followed the evening before to feeding areas in other parts of the city.

On the Ambassador Bridge the Starlings roost on ledges on the concrete bridge supports, where they have no roof above them, and on beams below the bridge, where they have a roof above them but no protection on the sides or below. Those on the outer structures do not perch in contact with each other, but maintain a regular individual distance. In the roost on the Wayne State campus the birds congregate on beams just below the roof overhang on the outside of the building, as well as inside the attic. It is much warmer inside than out, and there is much space available inside, but the Starlings remain mostly at the edge of the attic, where they may pile on top of each other, several deep. The accumulation of birds at the edge of the attic leaves much apparently suitable roosting space unoccupied. Even after dark the birds call noisily as they climb over each other on the perches, settling down for the night. In the winter the birds tend to crowd into tight places were they have close physical contact with the building structure and with other Starlings. During the summer, however, when there are fewer birds at the roost, they seem to avoid contact with each other, although they continue to perch in corners and in beam joints in the attic. This difference in behavior was especially noticeable because in winter the birds could be picked off the perches by hand easily, offering almost no resistance, whereas in the late spring and summer months they were spaced farther apart and moved away when they were touched, making capture much more difficult.

When flashlights were turned on in the Mackenzie Hall roost the birds flew about in an erratic manner, fluttering from beam to beam and into the light. Those birds perched near the openings to the outside often took flight from the roost. At first the birds were captured by attracting them to the light, but it was found that they could be obtained in greater numbers and more easily by crawling to the edge of the attic in the dark and simply picking them off their perches. This procedure resulted in little disturbance to the roost as a whole. Occasionally when caught the birds gave a loud alarm call, which usually caused some other roosting individuals to fly, but it did not cause an exodus of the whole colony, nor prevent the subsequent return of many individuals to the roost.

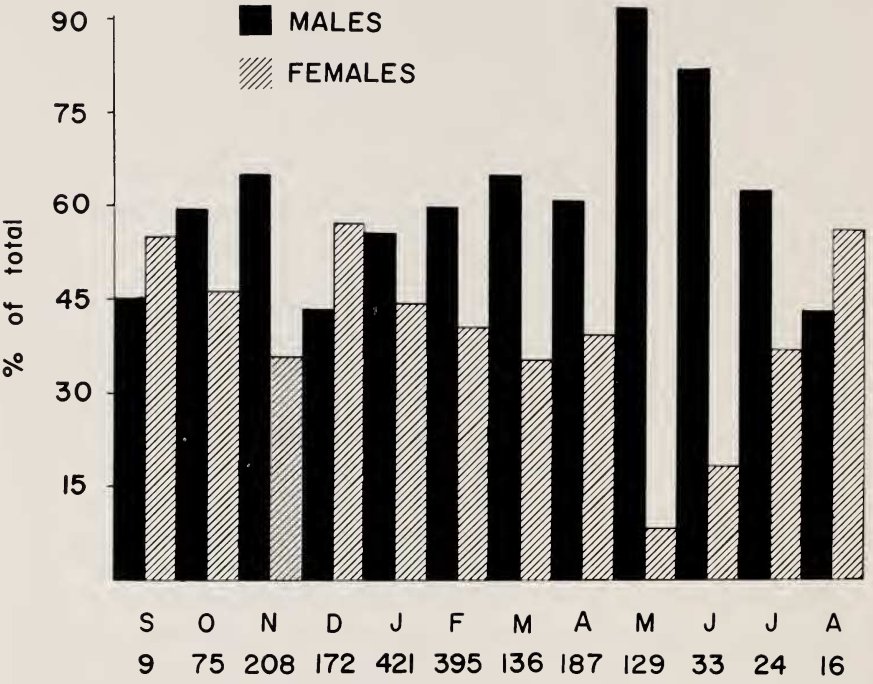

FIG. 1. The percentages of male and female Starlings at the Mackenzie Hall roost by months throughout the year.

The Mackenzie Hall roost was used, also, by feral pigeons nesting there throughout the year. No birds other than the Starlings and pigeons were found there.

STARLING POPULATION STRUCTURE

Sex and age composition of roosting population.—Birds picked off their perches were placed in burlap bags and carried to a room below the attic, where they were weighed, sexed, banded, and plucked of a few hackle feathers for later age determination. They were then released through an open window. At least some returned immediately to the roost, as was shown by our sometimes catching them again later the same evening.

No actual counts of birds at the Mackenzie Hall roost were attempted because of the confusion of birds entering, and because the number of birds roosting outside the attic could not be determined. Nevertheless, a rough approximation of the number roosting inside at different times was obtained from photographs. On the basis of these we estimate that during the cold winter months, from November through February, slightly more than 1,000 Starlings occupy the roost. The number drops to about 25 during the late

summer months of August and September, when many Starlings occupy communal roosts in trees in suburban areas.

Birds were sexed by iris and bill color differences as described by Kessel (1951) and Davis (1959). The length of the iridescent portion of hackle feathers was used as an index of age, also as described by Kessel and Davis. The percentages of males and females in the roosting population at the Mackenzie Hall roost throughout the year are shown in Fig. 1. The samples suggest marked fluctuations in numbers of males and females from month to month. These fluctuations are possibly due to sampling errors and may not reflect any actual discrepancies in sex ratios at the roost. If they do reflect actual fluctuations in the population as a whole, we cannot account for them. The marked decrease in number of females during May and June, however, probably does represent a real change in the composition of the roosting population, since we would expect to find the breeding females at their nests instead of at the communal roosts at this time of year. This may also account, at least in part, for the gradual, rather steady decline in number of females noticed from January through April.

Delvingt (1961*a*) cites a classification by Carrick of the stages of the bill coloration cycle from the yellow of the full breeding condition to the black of the refractory period, and back again to yellow. The data presented here have been arranged in a slightly different way, Carrick's six stages having been grouped into four. The timing of the color change is of particular interest because of the marked difference in the rate of change within the roosting population in the spring and summer. The transition from the black of the late summer and fall to the full yellow of winter and spring is gradual, but the change from yellow to black in late summer is very abrupt. Figures 2 and 3 indicate that males and females undergo these changes in bill coloration at about the same time, although there is a slight lag in the change of the female bill to its characteristic breeding coloration. The increase in number of black-billed females in January shown in Fig. 3 may be due to sampling or may represent a change in the composition of the roosting population. Delvingt (op. cit.), too, found that females lag behind males in change of bill color from black to yellow, and, also, that young birds of both sexes assume the yellow bill later than adults. We do not have enough data to analyze age differences in rate of change. Witschi and Miller (1938) indicate that the winter color change from black to yellow takes about two months in wild Starlings in Iowa. Since the color of the horny bill covering does not change once the pigment has been deposited during formation of the covering by the stratum germinativum at the base of the bill, a change in bill color can occur only by wearing away of the old covering at the tip and its replacement by a new, differently colored horny covering at the base. Witschi and

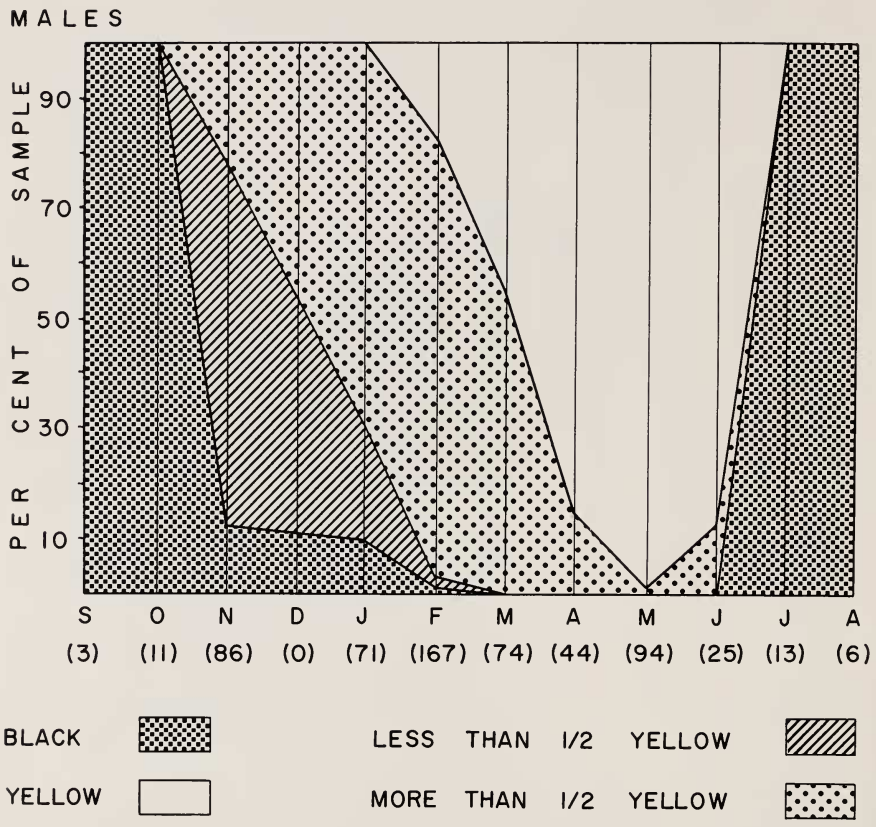

FIG. 2. Annual bill color changes in male Starlings captured at the Mackenzie Hall roost, by months.

Miller do not indicate whether the reverse change takes the same amount of time, although their lack of comment would seem to indicate that they believed it does. Nichols (1945) recorded a much more gradual change from yellow to black in the summer than our records show, but there is a suggestion in his data, also, of a more rapid change in summer than in winter.

We can account for the differences we observed in rate of change of bill color in spring and fall in at least two ways. Either there might be more rapid wear and replacement of the bill covering in summer at the time of molt than in winter, or the birds using the roost in summer may represent a primarily nonbreeding segment of the population. It is possible that a rapid growth of the horny bill covering occurs at the beginning of the molt, and that the overhang of horny material beyond the bony portion of the bill simply wears away faster than at a slower growth rate. Studies of individual

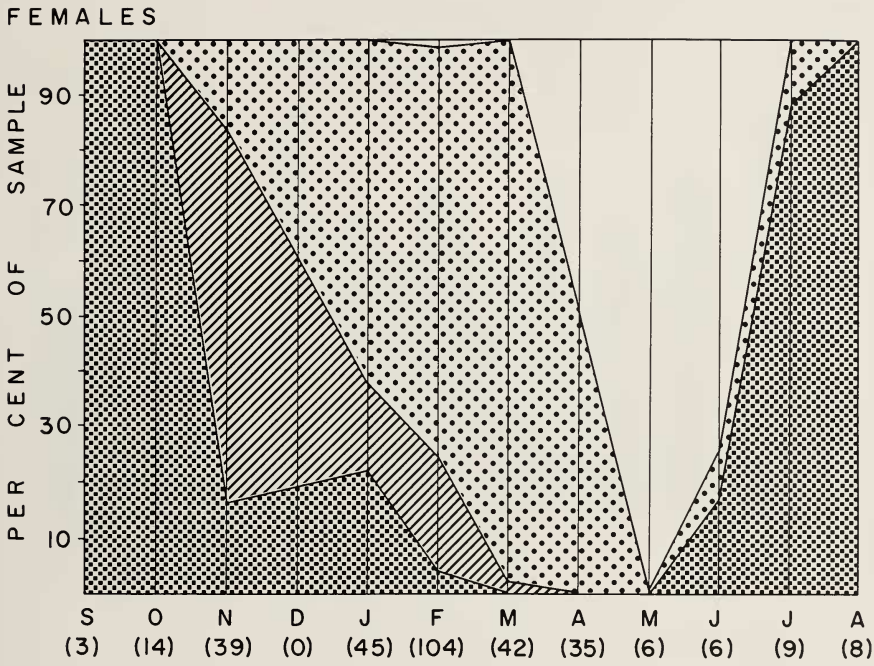

Fig. 3. Annual bill color changes in female Starlings captured at the Mackenzie Hall roost, by months.

wild Starlings would be necessary to determine whether this can account for the rapid change in bill color seen in the roosting population.

At first glance, and in view of Nichols' observations of bill color change in New York Starlings, the second alternative seems more likely, but still it is difficult to account for the abruptness of the change in fall. Why should breeding birds which have been using the roost suddenly stop using it, and just as suddenly be replaced by others which have been roosting elsewhere, and which have completed the two-month period presumably necessary to change from yellow to black? There are few individuals involved in these midsummer samples, but the inadequate sample size is not a satisfactory explanation of the problem, since the sample seems to represent a large fraction of the birds occupying the roost at that time. From the data available it is not possible to resolve the question. We need more evidence from the Detroit population as a whole, including birds not using the roost.

It has generally been found that Starling populations have an unbalanced sex ratio in favor of the males (Kessel, 1957; Davis, 1959; and Coulson, 1960). On the basis of our combined data for all seasons of the year the percentages of males and females at the Detroit roost were 60.7 per cent and

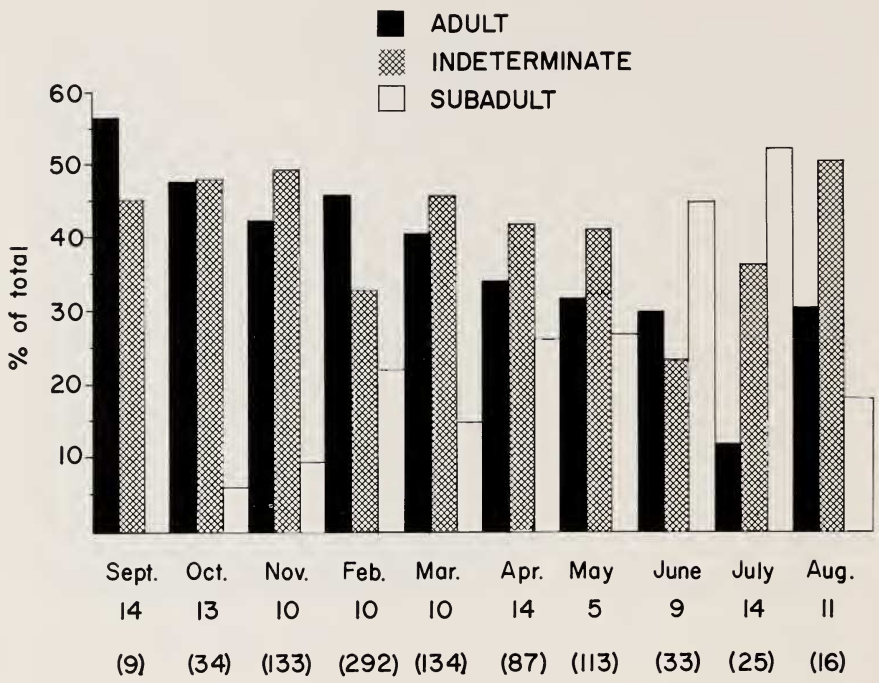

FIG. 4. Age composition of the roosting population of Starlings throughout the year.

39.3 per cent, respectively. It is apparent, however, that since during the breeding season the percentage of females at the roost drops markedly, lumping the data for all seasons would give a false impression of the sex composition of the Starling population at large. Using the data from November through March as Davis (op. cit.) did in calculating sex ratios of roosting Starlings in Baltimore, we obtain 56.6 per cent males and 43.4 per cent females.

At the Baltimore roost Davis found that the subadults, or first-year birds, had a more balanced sex ratio than the adults. Presumably, then, the females have a higher mortality rate after hatching than do the males. Coulson (1960) has suggested that this greater female mortality results from more females than males breeding during their first year and in being more subject to predation while nesting. We did not begin aging the Starlings until February of the second year of our study period, and so we do not have data on birds of known age for the entire period from November through March. For 96 subadult birds banded in February, March, and November of 1961, however, ratios of 64.6 per cent males and 35.4 per cent females were obtained. For 240 adults examined during the same period the ratios are 62.4 per cent and 37.1 per cent females. The sex ratios of the two age groups are approximately

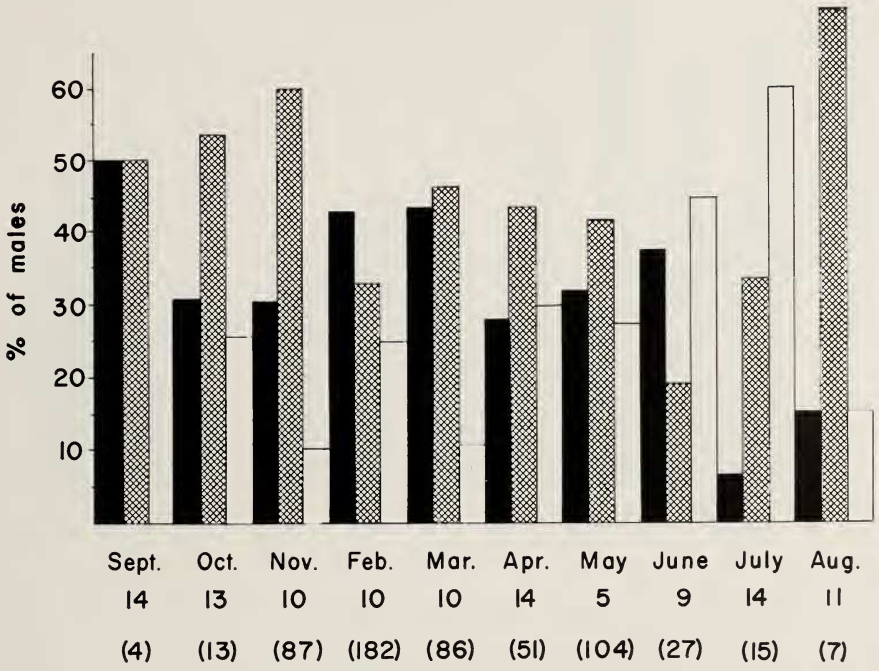

FIG. 5. Age of male Starlings occupying the roost at various times of the year.

the same, unlike the situation in the Baltimore roost studied by Davis, or the British banding records examined by Coulson.

Changes in age composition of the roosting population throughout the year are shown in Fig. 4. There is a noticeable decline in the proportion of adults occupying the roost during the breeding season, followed by an increase in the fall. There is a corresponding increase in the proportion of subadults from fall through the next summer. The abrupt decrease in proportion of subadults in late summer is presumably due to their molting and moving into the categories of indeterminate or adult, according to their feather structure. Likewise, the rapid increase in the proportion of indeterminate birds in late summer doubtlessly results from recruitment from the ranks of the subadults of the previous season. It appears from Fig. 4 that birds of the year do not begin to occupy the communal roost until fall, when the number of individuals of all age groups using the roost increases, and when the large flights to the roost begin.

Figures 5 and 6 reveal some differences in the age composition of the male and female segments of the roosting population. Whereas in the fall and early winter there are more males of indeterminate age than adults, there are more

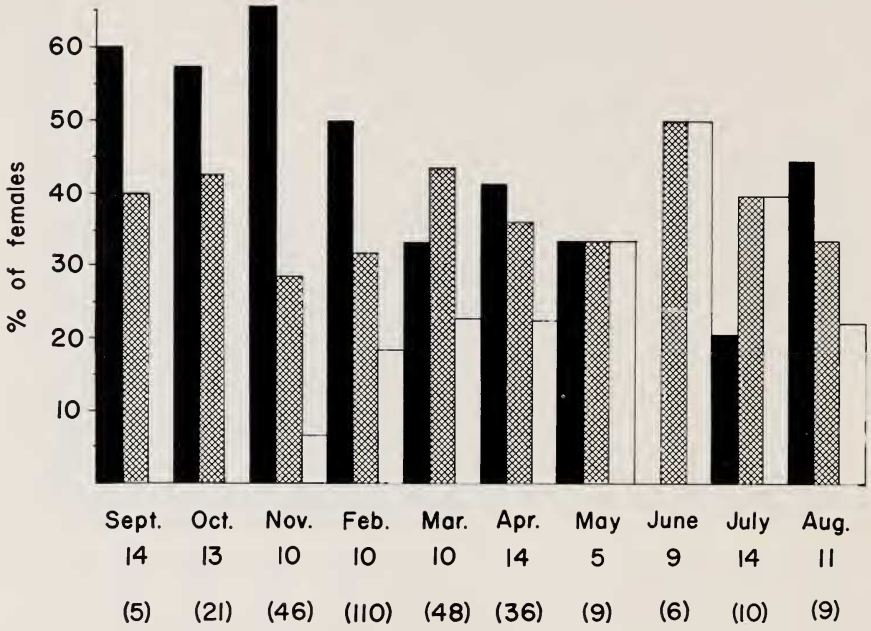

FIG. 6. Age of female Starlings occupying the roost at various times of the year.

adult females than indeterminates. These proportions suggest that, as Kessel (op. cit.) found, some adult males begin to occupy nesting territories in the fall and roost in the nest holes. The females, on the other hand, may not begin to roost in nest sites until much later, in early spring.

Although the increased proportion of subadult and indeterminate females on the roost during May and June might seem to suggest that some female birds less than one year old do not breed, the presence of a bird at the roost does not necessarily mean that it is not breeding, for we found one female roosting in Mackenzie Hall which had a well-developed egg in the oviduct, detected by palpating the abdomen. Witherby (1930) also found females in breeding condition at a communal roost in spring.

Seasonal weight fluctuations.—Birds were weighed routinely throughout most of the two-year study period. Each Starling was placed in a cardboard tube to be weighed. The weight of the bird was determined by substracting the weight of the tube from the total. Figure 7 shows the seasonal variation in weight of males and females. Each narrow vertical line represents the range of variation of the sample, while the wide vertical line indicates twice the standard error of the mean to either side of the mean, and the horizontal line represents the mean of the sample. Both males and females are signifi-

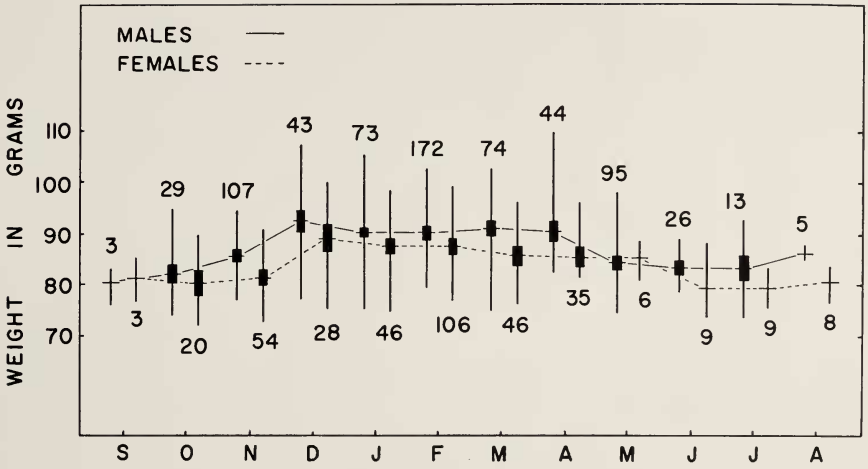

FIG. 7. Seasonal variations in weight of male and female Starlings occupying the roost, by months.

cantly heavier during the winter than during the summer, but there is considerable overlap in the range of variation. The minimal weights remain about the same during all seasons, but the maxima are higher in the winter than in the summer.

The lower summer weights could be due to several different factors, including a decrease in the number of breeding adults and a proportionate increase in the number of subadults and indeterminates. We have data on the weight variation in different age groups for only one year, but Fig. 8 indicates that the same pattern of seasonal variation is found in the subadults as in the adults. Following the late summer molt, either postjuvenal or postnuptial (prebasic of Humphrey and Parkes, 1959), the birds gain weight until they reach a maximum in early winter. This weight is maintained, with minor fluctuations through the winter, until spring, when it declines, reaching a minimum shortly before or at the time of the annual molt.

BANDING RETURNS AND RECOVERIES

During the period of study from December 1959, through November 1961, a total of 1,872 Starlings was banded at the Mackenzie Hall roost. Of these, 169 were recaptured there at some date subsequent to their first capture. This seemingly small return, only about 9 per cent, may be explained by assuming that we are dealing with a large, stable population of birds which uses the roost regularly, or by assuming that the roost is occupied by a constantly changing assemblage of birds from night to night. The second

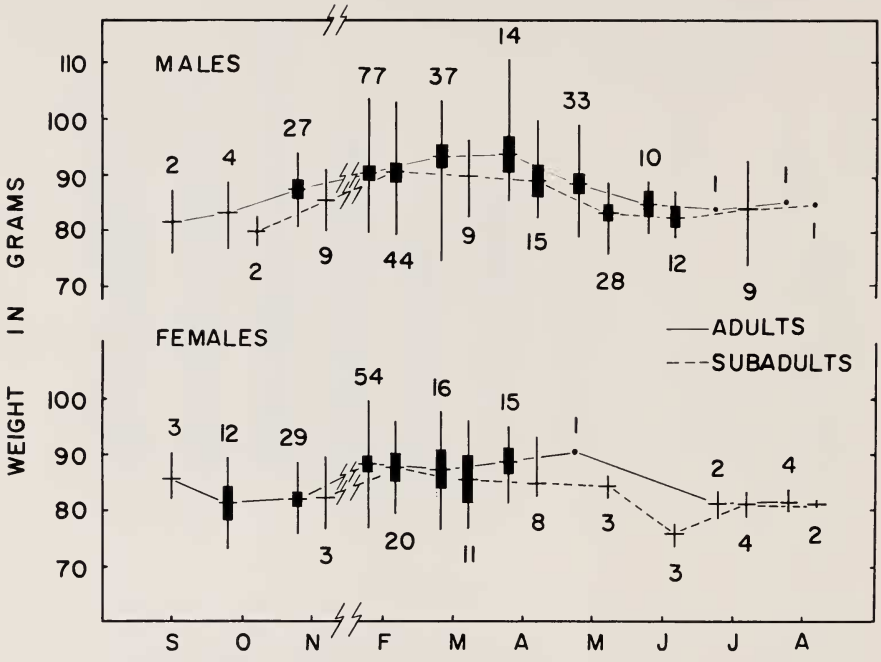

FIG. 8. Seasonal variations in weight of adult and subadult male and female Starlings occupying the roost, by months.

explanation appears to be the correct one because, if the population were stable, we would expect the number of recaptures to increase each time we visited the roost, but this was not the case. It is quite possible, of course, that the experience of being grabbed off the roost, thrust into a bag full of other birds, weighed, plucked of a few hackle feathers, banded, and finally tossed out a window discourages the banded birds from returning. If so, we might expect a decrease in the number of birds using the roost after each of our banding excursions, but no such decrease was apparent.

The evidence suggests that even if birds do return to the roost, they do not usually return to a given spot. One exception to this was a female taken in the same general area during banding sessions in three successive months. We usually took birds from parts of the roost which had the greatest concentrations of individuals, and this practice would tend to increase the likelihood of recapturing marked individuals if there were a strong tendency for birds to return to particular places each night.

It seems, then, that the Mackenzie Hall roost is occupied by a constantly changing population of Starlings. If our banding operations did disrupt what would otherwise have been a stable population, and thus produced this rapid

turnover, the places of those birds which left evidently were taken by others, thus maintaining a fairly constant number of birds occupying the roost from time to time, the actual number depending on the season.

As is usually the case, the number of reported recoveries of banded individuals away from the banding site was very small. Only 23 of the 1,872 Starlings banded have been reported to date. One bird banded in Memphis, Tennessee, was recaptured at the Mackenzie Hall roost. Except for this Starling which had traveled a distance of at least 590 miles, all the other birds banded at the Detroit roost have been reported within a radius of 200 miles, and all north of the roost.

Judging from the recovery data, the Starlings which occupy the Mackenzie Hall roost are mostly from local breeding populations. Some, however, are from breeding populations a short distance to the north and east. This agrees with Kessel's (1953) diagram of the main migration route of Starlings in the Midwest. According to her map, Starlings from southern Ontario pass around the west end of Lake Erie, and would thus come through the Detroit area. Several of our winter-banded birds have been recovered in southern Ontario in the spring and summer.

DISCUSSION

It has been demonstrated for several species of birds that the ability to survive the rigors of severe winter weather depends not so much on the birds' ability to withstand cold, per se, as on the availability of food, since birds probably can maintain their normal body temperature if their energy supply is maintained. It would appear, on the basis of Fig. 7, that the Detroit area Starlings are able to find an adequate food supply in winter, since they reach and maintain their peak body weight during the coldest months. The annual cycle of the Starling is well suited for winter survival. Reproductive development begins as early as November, although nesting does not actually begin until April. The most energy-demanding periods in the annual cycle of most birds are the rearing of young and the annual molt, and these are usually timed to coincide with seasons when there are rich food resources available. For the Starlings in the Detroit area the care of young is completed by the middle or the latter part of June, and the molt begins in July. It is completed by September, which leaves two months for the birds to build up their fat reserves before the severe, cold weather comes.

The immediate stimulus for leaving the feeding areas and flying toward the roost remains obscure, but probably involves light intensity, as Jumber (1956) suggests. Once in the vicinity of the roost, however, the birds seem to be responding more to social stimuli than to be seeking warmth and protection from the cold. It was mentioned earlier that some individuals often

leave groups flying toward the Ambassador Bridge to join birds already perched near or flying about the Mackenzie Hall roost. After their arrival in the vicinity of the roost the birds usually congregate on conspicuous perches until a large number has assembled, and then they fly together to the main roost shortly after the sun has set, and it begins to grow dark. Late arrivals reaching the vicinity of the roost at this time go directly to the roost without such preliminaries.

There can be no doubt that the sheltered, warm environment provided by a roost, such as the attic of Mackenzie Hall, is of great advantage to the Starlings during the winter. Any means of reducing heat loss, and thereby conserving energy, is of great benefit to birds and may enable them to survive during very cold weather, when their energy intake is likely to be low and their energy expenditure in maintaining body temperature is very high. The Starlings not only utilize shelter, but they sometimes also perch side by side, in contact with others around them, and sometimes piled several deep. For those in the middle of the mass of roosting birds the heat loss must be small, and even for those at the periphery the heat loss must be considerably reduced by having so many warm bodies close by. Thus, it is not only the shelter but also the presence of many other Starlings that is advantageous. Communal sleeping places are known to be used by other birds (Welty, 1962: 127; Frazier and Nolan, 1959; French, 1959; and Knorr, 1957) and mammals (Sealander, 1952) in very cold weather, and in these the practice presumably conserves energy stores by reducing heat loss. It is interesting to note that, as Delvingt points out (1959), continental European Starlings do not roost in masonry constructions, but usually in trees or vines. Large numbers of birds roosting together in evergreen trees with a dense foliage would be partly protected from the wind, and probably would provide some mutual protection from the cold. In England, in the late nineteenth century, Starlings began to occupy buildings in London. The practice of roosting in buildings was soon established in the United States by the descendants of the stock introduced from England.

At Mackenzie Hall the Starlings apparently seek physical contact with other birds at the edges of the attic, near the openings to the outside through which the wind whistles on cold, windy nights, leaving the warmer interior of the attic virtually empty of roosting Starlings. The number of birds roosting on the rafters outside under the roof has not been counted, and it may well exceed the number inside. There, the primary protection afforded by the building seems to be a roof above the perch, since the birds roost on the exposed north and west sides, as well as on the more protected south side. There is room for many birds to perch side by side, however, and they may provide some mutual protection and warmth. On the Ambassador Bridge, where there is much more space available for perching, the Starlings apparently

do not perch in contact with each other. They maintain an even spacing on the exposed outer ledges and beams that they occupy. During severe weather, however, most of the birds roost on beams under the bridge where they are not visible from below and it is not possible to determine how they are spaced on these perches. It is unlikely that the birds on the outer perches derive much thermal benefit from their neighbors, or from the bridge itself. Those underneath, however, are probably more protected.

Birds which gather in great roosting aggregations in summer and early fall, such as Starlings, redwings, and grackles, must derive no energetic benefit from their numbers and proximity. Such roosting habits must be explained in other ways. Lack (1954) has reviewed the evidence for protection from predation which flocking affords, but Delvingt (1961*b*) pointed out that predators are successful in raiding Starling roosts. It seems then that we cannot explain the advantage of social roosting to the birds in summer in terms of energy conservation or protection from predators, and yet it is difficult to believe that there is an entirely different motivation for summer and winter roosting because the flocking behavior is so similar at the summer and winter Starling roosts. The strongly social behavior of the birds at the roost suggests that the proximal stimuli are largely social and are not concerned entirely with finding a warm place for the night, although Marples (1934) has given some evidence for warmth as a primary factor in the choice of roosting sites by some British Starlings, and individual Starlings often perch on house chimneys on cold days, taking advantage of the heat coming out. It appears that a combination of factors is involved in the choice of roosting site. The site must be large enough to accommodate many birds, and it must offer some protection. The large summer and winter aggregations, with their rather ritualized preassembly and concerted movement to the roost, exhibit a marked gregariousness and social cohesion. It would be unwarranted to state that social attraction is the only factor involved in the choice of roosting sites. Still, even in midwinter, groups of birds may roost on exposed masonry ledges, protected by a single wall, exposed on three sides to the weather. It surely cannot be warmth alone which draws them together. It seems likely that once the strong antipathy to others of the same species shown during active defense of territory wanes, the social tendencies gain the ascendancy. This change is not a simple hormonal one, if such a change can be considered simple, because even breeding birds may resort to communal roosts, thus alternating territorial and social behavior within a single day. Even though the aggregations of birds in the summer and fall may provide for no energy gain, the gain obtained during the winter may be sufficiently great, at least in birds such as the Starlings, which spend the winter in cold climates, to perpetuate the sociality in other times of the year through natural selection.

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